

An Unusual Submerged Aquatic Ecotype of *Asplenium unilaterale*

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Although many ferns inhabit moist places, extremely few are actually deserving of the term aquatic. There are the floating miniferms *Azolla* and *Salvinia*, and others that usually root in mud with a fluctuating water level, e.g., *Ceratopteris*, *Acrostichum*, and Marsileaceae. Rheophytes, subject to floods in streambeds, are periodically aquatic. Some plants are moistened with constant spray from waterfalls (Giesenhagen, 1892; Mickel, 1972; Iwatsuki, 1975; Page, 1979). A species of *Stenochlaena* lives in water pockets formed by *Pandanus* leaf bases (Price, 1982, p. 200).

This report of *Asplenium unilaterale* Lam. makes it the second known fern that lives as a genuine submerged aquatic. The other such is *Bolbitis heudelotii* (Fée) Alston of Africa, sometimes cultivated in tropical aquaria, although it is merely a form of the species that is most often rheophytic (Hennipman, 1977, p. 236-240). *Asplenium unilaterale* is already known to be highly variable in cytology (Lovis, 1973), reproduction (Murakami & Iwatsuki, 1983) and habitat and morphology (Iwatsuki, 1975), with some plants (var. *udum*) having an extremely thin (bistratose) lamina lacking intercellular spaces.

The submerged form was collected in Seram (Ceram) Island, the Moluccas, Indonesia, during field trips in 1983 and 1984-85. On the island, ecologically and reproductively different forms of *Asplenium unilaterale* also are terrestrial or on dry or wet rocks in montane forests, as they are in the entire range. The new form grows in a spring named "Air Mata Makariki" at 350 m above sea level on the southern slope of Murkele Mountain Ridge at the central part of the island. This area is abundant in limestone rocks, and river water occasionally underflows. The spring is formed at the mouth of an underflowing stream and water flows out with air bubbles from the bottom of the spring at several points and goes down rapidly along Wae (=River) Makariki (Fig. 1). The water level appeared to be constant and the water temperature measured 19°C. The spring is surrounded by steep slopes covered by semi-primary forest. *Asplenium subnormale*, a lowland species closely related to *A. unilaterale*, was found growing terrestrially on the slope, but *A. unilaterale* was absent there.

The submerged form consists of several populations, and all the individuals are uniform in morphology. The largest population grows submerged 50-70 cm (to the top of the leaves) below the water surface in rather slowly flowing water, with numerous air bubbles, and epiphytic on likewise submerged roots of two trees of *Ficus* sp. (one ca. 28 cm and another 33 cm in DBH) which stand in the spring (Fig. 1). Smaller populations grow more shallowly submerged on roots

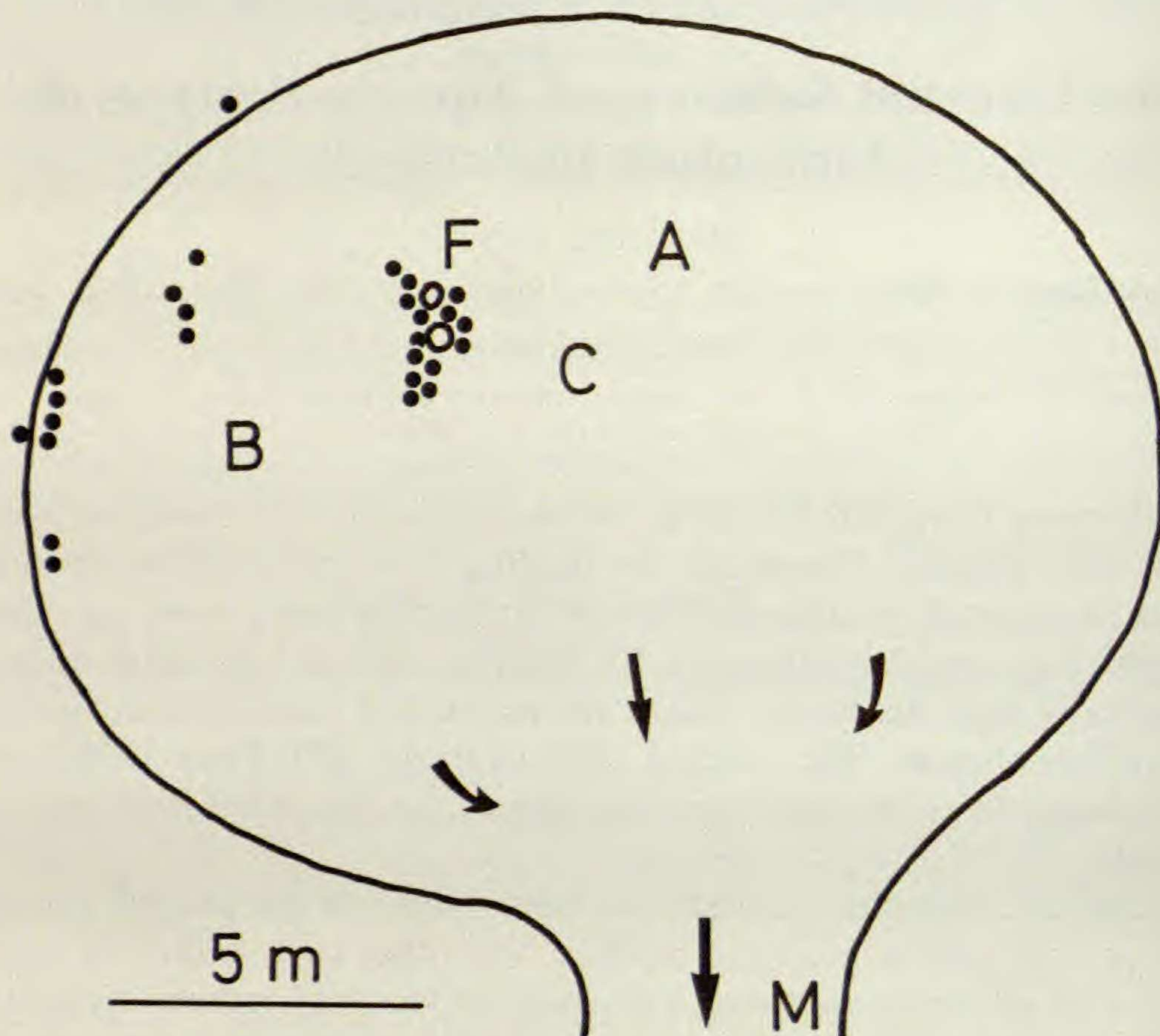
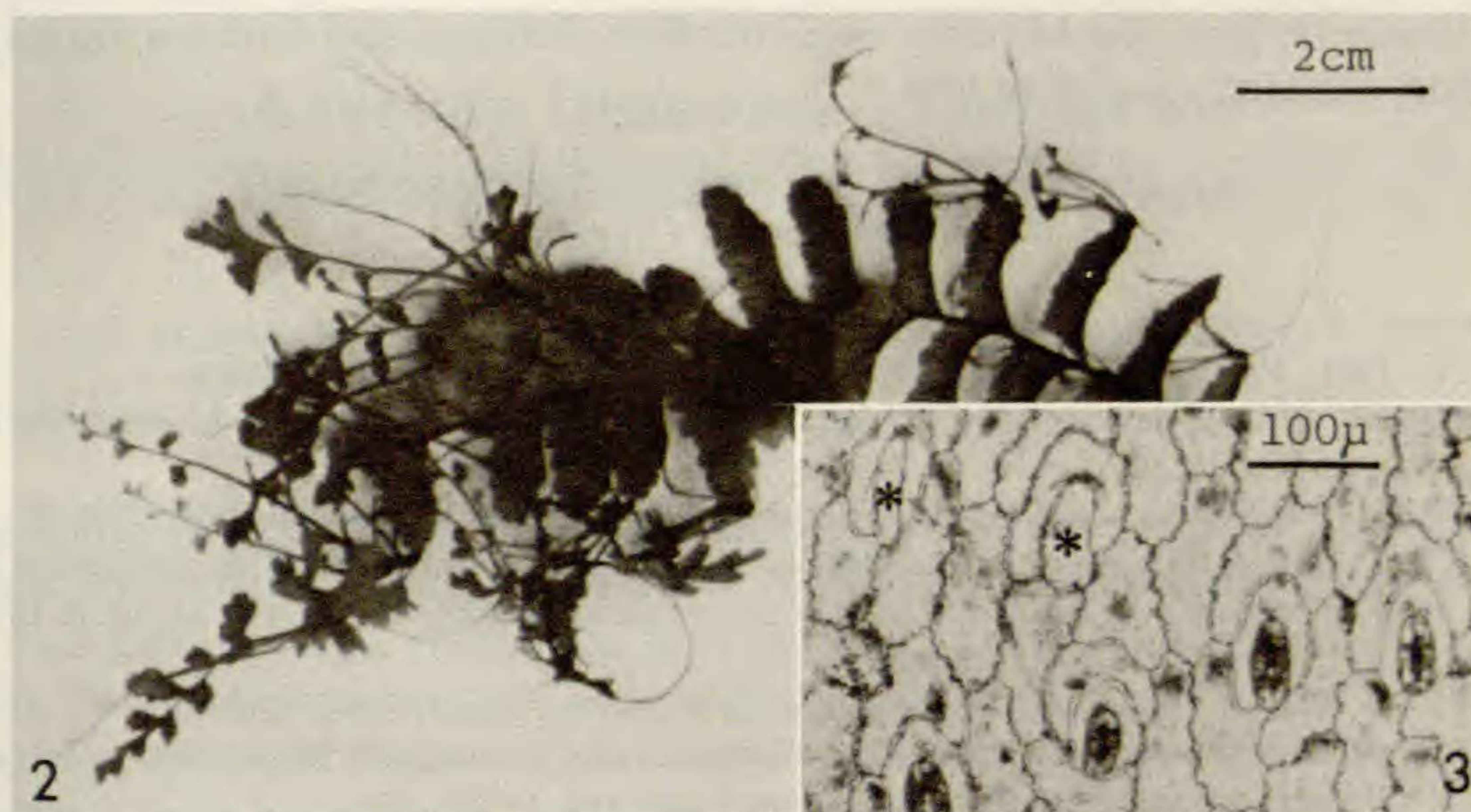


FIG. 1. Diagram of the spring "Air Mata Makariki." A, B: two largest water-flowing mouths. C: the deepest point (ca. 2 m deep). F: two trees of *Ficus* sp. M: Wae (=River) Makariki. Solid circle: individuals of the submerged aquatic ecotype of *Asplenium unilaterale*. Arrows indicate water flow.

from trees on the slope, or among rocks at the bottom of the spring. The smallest populations, which consist of a few individuals, grow on tree roots and in rock crevices, both beside the spring, slightly above the water surface.

The submerged form differs from the terrestrial only in the following combination of characters: rhizomes are rather long-creeping, branching, and bearing long slender branched roots, altogether constituting an entangled rhizome-root system. Detached leaves or pinnae are trapped by the rhizome-root system, and new plants anchor and grow in the system (Fig. 2). Anatomical features of the roots do not differ from those of the terrestrial forms. Gemmae are profusely borne and develop into young plants on pinnae, whereas the terrestrial forms are usually not gemmiferous. However, plants that were transplanted in pots in a greenhouse in the University of Tokyo Botanical Gardens in 1983 have so far not produced any gemmiferous leaves.

In the aquatic form, the apices of pinnae are broadly obtuse as compared with subacute apices of the land forms. Anatomically the pinnae consist of an upper epidermis, a mesophyll of spongy tissue and a lower epidermis with stomata, as in the land forms, but 10-20% of stomata are incomplete (Fig. 3). Newly developed leaves of two-year-old plants cultivated in soil in pots retain this feature. Each sporangium, a typical leptosporangium of the terrestrial *Asplenium unilaterale*, produces approximately 32 spores, some of which are abortive, with the



FIGS. 2, 3. Submerged aquatic *Asplenium unilaterale*. FIG. 2. Leaf bearing young plants developed from gemmae. FIG. 3. Surface view of a lower epidermis. Asterisks indicate incomplete stomata.

same exospore ornamentation as that of the terrestrial form. The number suggests an ability to be apogamous.

In contrast to species of aquatic ferns that are distinct morphologically and taxonomically, the submerged *Asplenium unilaterale* retains the morphology for land life and is considered to be an ecotype or a local form at the early stage of quantum speciation (Grant, 1981). The peculiarly submerged aquatic life seems to be facultative in the presumably recently formed habitat. This assumption is based on the small morphological differences such as incomplete development of some stomata between the submerged and land forms, and the recent origin of the spring which is suggested by the occurrence of the *Ficus* sp. trees in the spring.

Another noteworthy aspect is reproduction of the submerged form. The vegetative reproduction by pinna-borne gemmae that grow into new plants anchoring in the rhizome-root system may be the most suitable means for the fern in question to remain completely submerged in the flowing water. It is a substitute for reproduction by spores and gametophytes which, even if apogamous, might not be possible for this fern, because freely dispersed spores are easily washed away in flowing water. Since such vegetative reproduction occasionally takes place in the terrestrial *Asplenium unilaterale* in Seram Is., it is a phenotypic variable that is merely strongly expressed by the aquatic form. A parallel development is the possible induction of adventitious buds in a saturated atmosphere in the filmy fern *Trichomanes minutum* (Yoroi & Iwatsuki, 1977).

The origin of the submerged form remains to be clarified, but it may be suggested that when the spring arose, the aquatic ecotype was derived from one of the possibly apogamous land forms that occur on Seram Island. Biosystematic analysis of interrelationships among the infraspecific variants of *Asplenium unilaterale* on the island is needed.

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REVIEW

"*Index filicum. Supplementum quintum: pro annis 1961-1975*," by F. M. Jarrett, with collaborators. 1985. 245 pp. New York: Clarendon Press, Oxford University Press. ISBN 0-19-854579-7. \$39.95.

Students of ferns are familiar with the great value of this index, begun by that most illustrious of pteridologists, Carl Christensen, in 1905. It is the only comprehensive source for obtaining bibliographic citations (name and place of publication, plus basionym for new combinations and locality for new species) for all Latin names, generic rank and above. Thus, we are forever grateful to the compilers of this and all preceding volumes. A new and welcome feature of the fifth supplement is the inclusion of names of fern allies. Corrections from past indices are denoted by an asterisk. As helpful as this index will be, it will not satisfy all needs: continuing the tradition of past volumes, infraspecific names are not indexed. In evaluating genera with which I am most familiar, I found only a few minor errors and omissions (to whom should I send them?) that will no doubt be corrected in subsequent volumes. One parting lament—one wishes that this index were more current: in the last ten years, I extrapolate that enough new names have accumulated to fill about 165 pages of a new supplement!—

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